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Design and Prey Capture Ability of Webs of the Spiders *Nephila clavata* and *Argiope bruennichii*

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ジョロウグモとナガコガネグモの網のデザインと餌捕獲能力

Abstract The relationship between design and prey capture ability of webs was examined in the two orb-weaving spiders *Nephila clavata* and *Argiope bruennichii*. We collected unstressed webs of both species by framing them with large paper mounts, and exposed them at the same microhabitat. Webs of *Nephila* tended to capture more prey than those of *Argiope*, due to the larger number of sticky threads. However, the proportion of relatively large prey (2–6 mm) was greater in *Argiope*, probably due to the larger amount of adhesive material attached to the web silk. We conducted another experiment to assess the retention ability of webs for large prey (20–25 mm) by putting it on the web. The amount of time the prey remained trapped in the web was similar between the species, though the variation was large. We consider that the web of *Nephila* functions to capture large prey as well as very small prey.

Introduction

Diversity of web architecture in spiders has long been considered to reflect different prey capture strategy (*e.g.*, BRISTOWE, 1941, UETZ *et al.*, 1978, CRAIG, 1987). It has become evident that this relationship is complex and the general prediction of prey size composition cannot be made by the simple geometry of orb-webs (UETZ & BIERE, 1980, CRAIG, 1987, EBERHARD, 1986, 1990). When web placement and/or spider behavior differ between species, which is often the case in nature, it is virtually impossible to attribute the difference in prey composition to the web architecture alone without suitable experimentations. Several kinds of experiments were performed to clarify this relationship. One is to compare prey caught by artificial webs having different intervals of sticky threads (CHACÓN & EBERHARD, 1980, NENTWIG, 1983). The major defect of this experiment is the inability to mimic the strength and extensibility of web silk of actual spiders. Another experiment that was often conducted is to measure the strength and retention ability of webs with different designs (LUBIN, 1973, CRAIG, 1987). Even

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this method cannot evaluate precisely the function of the webs realized in the field, because size and taxon of potential prey influencing escaping ability from the web (LUBIN, 1973, NENTWIG, 1982, CRAIG, 1986, ENDO, 1989) are difficult to estimate. These shortcomings will be resolved partly when webs of different designs are collected and exposed to the same microhabitat in the field.

The orb-web spiders, *Nephila clavata* L. KOCH and *Argiope bruennichii* (SCOPOLI), are common in central Japan and coexist widely, although their preferable habitats differ to some extent (MIYASHITA, 1994). A previous study has shown that the size compositions of prey differed significantly between the species of similar body sizes (MIYASHITA, 1994). This, however, may not be due to the difference in web designs, since prey capture behavior as well as web placement also seem to be different. To clarify the causal relationship between web design and prey size, we placed webs of the two species at the same microhabitat and examined the prey size caught by the webs. Because large prey were not caught by the webs, we conducted another experiment to know the retention ability of the webs for large prey. Furthermore, we measured web and silk characteristics of the two species.

Materials and Methods

Field experiments were conducted in the Tokyo University Forest Experimental Station at Tanashi, Japan. This station has an area of about 10 ha and consists of large woodlands and small grasslands.

On October 1, 1994, we collected ten webs of each spider (*Nephila* and *Argiope*) around 10:00 in the morning. All individuals of the two species were in the adult stage, and the body lengths were 17–25 mm. Frames of 16 cm × 16 cm inside area made of cardboard were used for the collection. We first spread glue on one side of a frame, and then pressed the frame gently to the web from which the spider had been removed. Next, web silks outside the frame were cut and finally another frame was attached to the frame, *i.e.*, the web was sandwiched between the frames. In this way, we obtained unstressed webs framed by a paper mount. The framed webs were exposed in a small grassland using metallic poles and hemp strings. Five pairs of webs, each of which was composed of the two species' webs, were set at 130 cm above the ground, and the remaining five pairs were set at 60 cm (see Fig. 1). Just after the setting, the number and size of prey already glued to the webs were recorded. Number of sticky threads and radii of each framed web were also counted. The webs were exposed in the field from 10:30 am to 5:30 pm, and then brought to the laboratory to examine the size and taxon of prey caught. We also conducted direct observations of 16 webs for 3 hours to record the large prey hitting the web.

Since large prey were not caught in the above experiment, we conducted another experiment to assess the retention ability of webs for large prey for the two species. Naturally occurring webs from which spiders were removed were used in this experiment. A wasp *Campsomeris* sp. (20–25 mm in body length) was used as large prey because it was sometimes observed being eaten by *Nephila* and *Argiope* and was easily obtained from the flowers of *Solidago*. We dropped a wasp onto the web from 2 cm above, and recorded the amount of time it remained trapped in the web.

To know the differences in the silk structure between species, we collected five

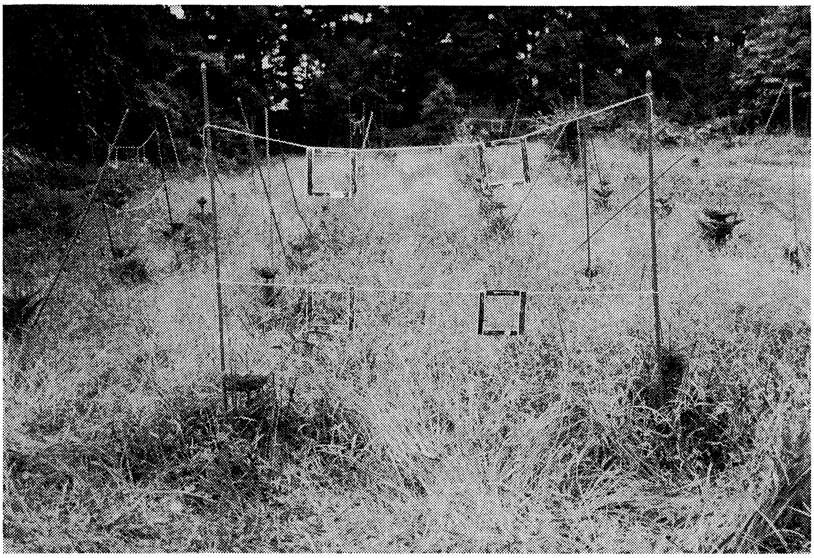

Fig. 1. Framed webs exposed in the grassland.

unstressed webs of each species by using a paper mount for slide film. The range of body length of spiders whose webs were collected was 17–22 mm in both species. The following silk characters were measured from the photos taken through a microscope: spiral diameter, radius diameter, number of droplets per 320 μm, and transverse diameter of the adhesive droplet attached to the spiral (magnification: ×150 for the number of droplets and ×600 for the rest).

Results

Prey caught by framed webs. During the 3 hours of observation of 16 framed webs, only one prey of about 4 mm (probably Brachycera) hit a web of *Nephila* and escaped immediately. Therefore, no information was obtained concerning the relationship between web type and capture success for large prey in this experiment.

A total of 53 prey were caught by the ten webs of *Nephila*, and 35 prey were caught by the ten webs of *Argiope*. Since numbers of prey were similar between webs set at higher and lower places (*Nephila*: 27 and 26 at higher and lower places, respectively; *Argiope*: 18 and 17 at higher and lower places, respectively), effects of height are not considered in the subsequent analysis. Mean number of prey caught per web tended to be greater in *Nephila* than in *Argiope* (Fig. 2, $t=1.78$, $p<0.1$). Number of sticky spirals was nearly two times greater in *Nephila* than in *Argiope*, which was highly significant (Fig. 2, $t=5.69$, $p<0.001$).

Size distribution of prey caught by the webs (ten webs pooled) are shown in Fig. 3. The distributions were significantly different between the two species ($\chi^2=8.18$, $p<0.05$). The proportion of prey larger than or equal to 2 mm seemed to be higher in *Argiope*.

The dominant prey taxa caught by the webs were Nematocera and Homoptera

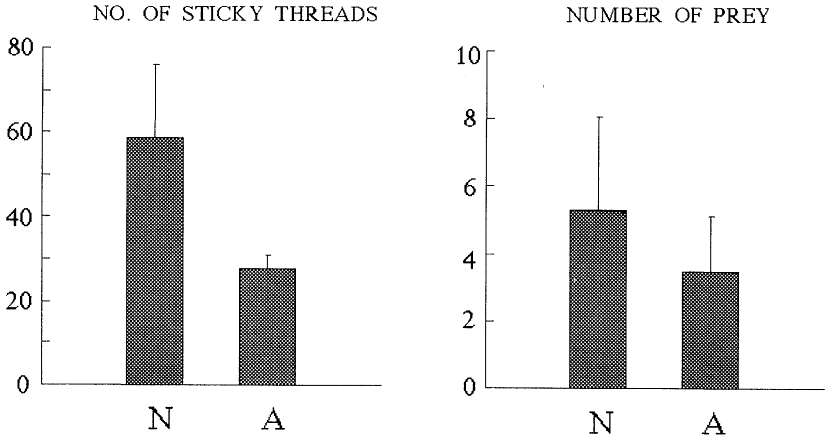

Fig. 2. Mean number of sticky threads per framed web and mean number of prey caught by the framed web of *N. clavata* (N) and *A. bruennichii* (A). Bars indicate SD.

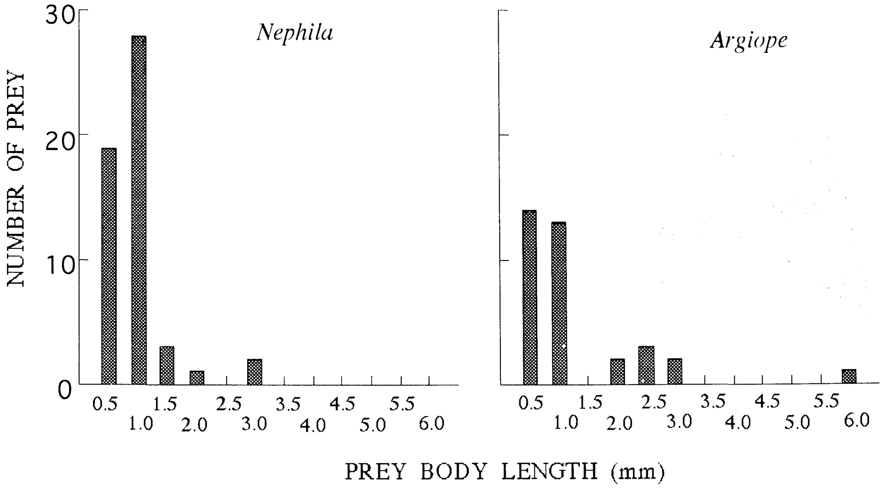

Fig. 3. Frequency distribution of the body size of prey caught by the framed webs.

(mainly aphids), which constituted more than 70% in both spider species (Table 1). Prey taxonomic compositions (Nematocera, Homoptera, Coleoptera, and others) did not differ significantly between the species ($\chi^2=1.66$, $p>0.6$).

Retention ability for large prey. Table 2 shows the median and range of retention time of webs for the large prey. The variation of the retention time of each species was so large that no difference was found between the species ($U=77.5$, $p>0.4$).

Silk characteristics. Figure 4 shows four silk characters in the two species. The droplet diameter of *Argiope* was 1.6 times larger than that of *Nephila* ($U=1.5$, $p<0.03$), whereas the number of droplets was about 2.1 times larger in *Nephila*

Table 1. Taxonomic composition of prey caught by framed webs. Values in parenthesis represent percentage to the total number.

Taxon	Number of prey	
	Nephila	*Argiope*
Homoptera	16 (30)	14 (40)
Heteroptera	0 (0)	2 (6)
Diptera		
Brachycera	2 (4)	1 (3)
Nematocera	23 (43)	13 (37)
Hymenoptera	3 (6)	2 (6)
Coleoptera	8 (15)	3 (9)
Araneae	1 (2)	0 (0)

Table 2. The amount of time a wasp (body length: 20–25 mm) remained trapped in the web of the spiders.

	Time (seconds)	
	Nephila	*Argiope*
Median	18	12
Range	4–300	5–75
N	10	13

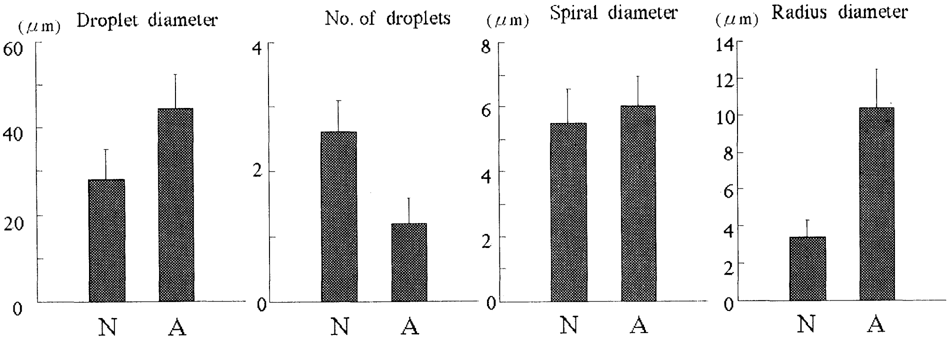

Fig. 4. Mean values of the four silk characteristics of *N. clavata* (N) and *A. bruennichii* (A). Bars indicate SD.

than in *Argiope* ($U=24$, $p<0.02$). The volume of the adhesive material per unit length of thread is roughly proportional to $D^3 \times N$, where D is the diameter of a droplet and N is the number of droplets per unit length. Thus, the volume of adhesive material of *Argiope* is about 1.95 times larger than that of *Nephila* $[(1.6)^3/2.1=1.95]$.

Spiral diameter did not differ significantly between the species ($U=9$, $p>0.4$), while radius diameter was much larger in *Argiope* ($U=0, p<0.01$). This is because the radius of *Argiope* was composed of two threads, while that of *Nephila* consisted mostly of a single thread.

Discussion

There have been many attempts to clarify the relationship between web design and its function in orb-weaving spiders in nature, but many of them could not control factors other than web characteristics (see EBERHARD, 1990), *e.g.*, local web placement, spider body size, and spider predatory behavior. The experiment using framed webs can obviously exclude these factors because webs are placed at the same microhabitat and no spiders are present on the webs. On the other hand, large prey rarely hit the web and if it happens, they will escape immediately; hence the estimation of the web function for large prey is extremely difficult by such an experiment. For the moment, we will refer to the capture ability for small prey (less than 7 mm).

The process for capturing prey at spider webs is divided into three steps: 1) intercept the prey, 2) absorb the kinetic energy of the prey (stop it), and 3) retain or adhere the prey (CHACÓN & EBERHARD, 1980, CRAIG, 1987, EBERHARD, 1990). Since prey captured in this experiment were small, the second step did not seem to affect difference in prey composition between species. The number of prey caught by the framed web of *Nephila* was about 1.5 times larger than that of *Argiope* (Fig. 1). This is clearly due to the larger number of sticky threads in *Nephila* (Fig. 1), *i.e.*, difference in interception ability. However, relatively large prey (>2 mm) seemed to be caught more frequently in *Argiope* (Fig. 2). Sticky silk of *Argiope* contained about twice as much adhesive material as that of *Nephila*, which must have compensated the low interception ability of *Arpiope*'s web. Namely, relatively large insects must have been glued to the silk of *Argiope* at the time of hitting, while most of them must have escaped from the *Nephila*'s silk after hitting. Thus, the web of *Argiope* appears to have an advantage for capturing relatively larger prey (7 mm$>$size$>$2 mm).

Although the number of small prey caught by the framed webs were numerous, one may be suspicious about the contribution of such prey to the total food consumption. NENTWIG (1985) reported that small insects that were not picked up individually by the spider comprised about 10% of the total prey dry weight in *Argiope argentata*, which were consumed later with silk at the time of web removal. MIYASHITA (1992) found that small prey ($\leqq 2$ mm) constituted nearly 30% of the total feeding time and were eaten relatively constant among individuals in *N. clavata*. Therefore, these prey may be essential for the spider especially in times of shortage of larger insects (NENTWIG, 1985, MIYASHITA, 1992).

The experiment using a wasp as a large prey revealed that the retention ability of webs did not differ between the species (Table 2). Factors affecting the retention ability of webs are adhesiveness of a single thread and number of threads adhering to a prey. The quantity of the adhesive of a thread of *Argiope* is twice as much as that of *Nephila*, while the number of threads are nearly twice larger in *Nephila* than in *Argiope* (Fig. 1). Consequently, it seems that the retention abilities of webs of the two species are roughly equal when large prey are entrapped in the web. In addition, we observed that wasps slowly rolled down on *Nephila*'s web as they struggled to escape. This makes it difficult for a wasp to escape, because when a thread detached from the body, another thread newly adhered to it. Such rolling down behavior was seldom observed in *Argiope*'s web, because the interval of the threads is large. Therefore, the fine mesh size of the web of *Nephila* might be designed to capture large prey as well as very small prey.

This study clarified the function of webs for small prey in the two species, but the function for large prey was not fully realized. Further experiments using various sizes and species of prey are necessary.

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摘　要

網のデザインと餌捕獲能力との関係をジョロウグモとナガコガネグモを用いて調べた．大型の厚紙のフレームでクモの網を枠取りし，同じ微生息場所に設置した．ジョロウグモの網はナガコガネグモの網より多くの餌がかかる傾向があったが，これは前種で粘着糸が多いからである．しかし，比較的大きな餌 (2–6 mm) の比率はナガコガネグモの方が大きかった．これはおそらく網糸に付着している粘着物質の量が多いからであろう．大型の餌 (20–25 mm) に対する網の捕捉能力を評価するため，大型餌を網に付加する実験を行った．餌が網に捕えられている時間は，ばらつきが大きいものの種間で似かよっていた．ジョロウグモの網は，非常に小型の餌とともに大型の餌を捕獲する機能も有していると考えられた．

References

BRISTOWE, W. S., 1941. The Comity of Spiders. Vol. 2, pp. i–xiv, 229–560, pl. 20–22. Ray Society, London.

CHACÓN, P., & W. G. EBERHARD, 1980. Factors affecting numbers and kinds of prey caught in artificial spider webs, with considerations of how orb webs trap prey. *Bull. Br. arachnol. Soc.*, **5**: 29–38.

CRAIG, C. L., 1986. Orb-web visibility: the influence of insect flight behaviour and visual physiology on the evolution of web designs in Araneoidae. *Anim. Behav.*, **34**: 54–68.

———— 1987. The ecological and evolutionary interdependence between web architecture and web silk spun by orb web weaving spiders. *Biol. J. Linn. Soc.*, **30**: 135–162.

EBERHARD, W. G., 1986. Effects of orb-web geometry on prey interception and retention. In SHEAR, W. A. (ed.): *Spiders, Webs, Behavior and Evolution*, pp. 70–100. Stanford Univ. Press, Stanford.

———— 1990. Function and phylogeny of spider webs. *Annu. Rev. Ecol. Syst.*, **21**: 341–372.

ENDO, T., 1989. How to avoid becoming a prey: Predator encounters between an orb-weaving spider, *Araneus pinguis* (KARSCH) (Araneae: Araneidae) and flying insects. *Ecol. Res.*, **4**: 361–371.

LUBIN, Y. D., 1973. Web structure and function: the non-adhesive orb-web of *Cyrtophora moluccensis* (DOLESCHALL) (Araneae: Araneidae). *Forma Functio*, **6**: 337–358.

NENTWIG, W., 1982. Why do only certain insects escape from a spider's web? *Oecologia*, **53**: 412–417.

——— 1983. The non-filter function of orb-webs in spiders. *Ibid.*, **58**: 418–420.

——— 1985. Prey analysis of four species of tropical orb-weaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone. *Ibid.*, **66**: 580–594.

MIYASHITA, T., 1992. Size composition of prey in the orb-web spider *Nephila clavata* estimated by video recordings and sight-count censuses. *Acta arachnol.*, **41**: 143–148.

——— 1994. What determines the local distributions of the two orb-web spider species?: inferences from the field experiments. *Appl. Entomol. Zool.*, **29**: 577–583.

UETZ, W. G., A. D. JOHNSON & D. W. SCHEMSKE, 1978. Web placement, web structure and prey capture in orb-weaving spiders. *Bull. Br. arachnol. Soc.*, **4**: 141–148.

——— & J. M. BIERE, 1980. Prey of *Micrathena gracilis* (WALCKENAER) (Araneae: Araneidae) in comparison with artificial webs and other trapping devices. *Bull. Br. arachnol. Soc.*, **5**: 101–107.